TWO NEW GENERA OF ACANTHODRILINAE (MEGASCOLECIDAE, OLIGOCHAETA) FROM CAPE YORK PENINSULA AND THE TORRES STRAIT

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Two new meronephric genera of Australian acanthodrile earthworms from Cape York Peninsula and the Torres Strait are described: *Neodiplotrema* gen nov., with seven new species, and *Torresiella* gen nov, with a single new species. All are considered to be local derivatives of the holonephric endemic Australian genus *Diplotrema*. Six species of *Neodiplotrema* show the acanthodrilin condition of the male genital terminalia, with male pores on segment XVIII and a pair of prostate pores on each of segments XVII and XIX, but one species exhibits the microscolecin reduction in which male pores have been translocated forwards to unite with a single pair of prostate pores, in XVII. Two species of *Neodiplotrema* have modifications of the nephridial system which pose difficulties for the existing classification of the Megascolecidae. *Torresiella* shows the rare balantine reduction in which the male pores have been translocated posteriorly to unite with a single pair of prostate pores, in XIX. □ *Acanthodrilinae, Megascolecidae, Neodiplotrema, Torresiella., oligochaete.*

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Prior to the present work, the Australian genera of earthworms of the subfamily Acanthodrilinae have been exclusively holonephric, with a pair of stomate nephridia in each typical body segment. In contrast, Lee (1959, 1970) clearly demonstrated close affinity between holonephric New Zealand acanthodrile genera and those with more than one pair of nephridia per segment, the meronephric condition, and concluded that local transition from holonephry to meronephry had occurred. Two meronephric genera of Australian acanthodriles are here described which are considered to be similarly localised derivatives of the endemic holonephric genus *Diplotrema*.

Diplotrema has been demonstrated to have an extensive range, from the vicinity of Narrabri, New South Wales, to northern Queensland and across northern Australia to the Kimberley region of Western Australia. (Mackenzie & Dyne, 1991; Jamieson & Dyne, 1976; Dyne, 1979). The precise northerly limit of the genus in Cape York Peninsula is unknown, the most northerly definitive record coming from the vicinity of Weipa (Dyne, 1984). It is thus uncertain whether *Neodiplotrema* effectively replaces *Diplotrema* from a certain point northwards. However, the two genera are sympatric in in the Cape Melville National Park and McIlwraith Range (Jamieson, 1997, this volume).

Despite recent efforts to improve knowledge of the biota of the region generally (e.g., Glasco et al., 1995), the earthworm fauna of Cape York Peninsula and the Torres Strait remains poorly understood. Apart from species of the pheretimoid genus *Begemius* described by Easton (1982), this paper constitutes the only account of endemic earthworm taxa from the region.

Abbreviations used. ANIC = Australian National Insect Collection, coll. = collected by, gm = genital marking, GD = Author's collection, H = holotype, P = paratype, pr. p = prostatic porophore, p.s.p. = penial seta pore, QM = Queensland Museum, Sp. p = spermathecal pore. Scale-bars = 1mm in all figures.

Neodiplotrema gen. nov.

DIAGNOSIS. Setae 8 per segment. Prostates 2 pairs, tubular, their pores on XVII and XIX, or, exceptionally, a single pair, on XVII. Male pores present in XVIII, or, rarely (microscolecin condition), closely associated with a single pair of prostatic pores on XVII. Spermathecal pores 2 pairs, in 7/8 and 8/9, or a single pair, in 8/9 only. Gizzard very well-developed, in V. Calciferous glands present or absent. Meronephric, avesiculate; anterior tufted nephridia present. Holandric, or, exceptionally, metandric. Testis-sacs absent. Penial setae invariably present; genital setae usually present, but occasionally lacking.

DESCRIPTION. Small to large terrestrial worms (48-465mm in length) with 130-500 segments. Body circular in cross-section. Prostomium pro-

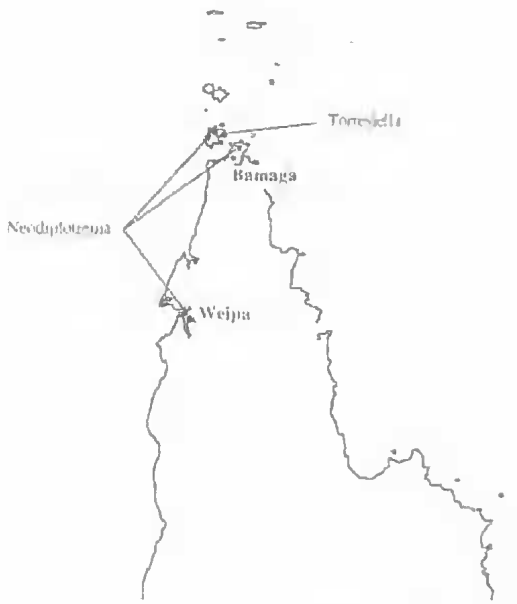

FIG. 1. Map showing recorded occurrences of *Neodiplotrema* and *Torresiella*.

epilobous to epilobous. Dorsal and median ventral groove absent. Dorsal pores commencing from 8/9 to 11/12. Setae closely paired, commencing on II; ventral intersetal distance (*aa*) not greatly different from that (*bc*) separating the lateral setae; ventral and dorsal setal couples of similar width; dorsal median intersetal distance (*dd*) > 45% of the body circumference in the forebody. Setae of XVIII, or the ventral setal couples lacking; ventral setal couples of XVII and XIX modified as enlarged penial setae, or, rarely, only those of XVII thus modified (in *N. deminutionis*); ventral setal couples of IX modified as enlarged genital setae, or undifferentiated. Nephropores numerous and usually inconspicuous. Clitellum saddle-shaped, or annular, occupying XIII to XVI-XVIII. Two pairs of prostatic pores, equatorial on XVII and XIX, coincident with the penial seta orifices, or (*D. deminutionis*) a single pair of combined male and prostatic pores on XVII. Male pores a pair of openings in seminal grooves (the latter well-developed or very faint), presetally, or far anteriad, in XVIII (rarely in the microscolecin arrangement). Accessory genital markings present in some of the segments VIII-XXXII, usually intersegmental, rarely absent. Female pores paired, presetal, median to lateral of *ab*, in XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in or near *ab*, exceptionally in 8/9 only.

Some pre-clitellar septa thickened. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, some of the commissurals posteriad of and including X latero-oesophageal, dorso-ventral commissural vessels commencing in VI-VII; supra-oesophageal vessel limited to the oesophagus; subneural vessel absent. Gizzard large, often strongly muscular, in V. Calciferous glands absent, or developed as sessile pouches in the posterior oesophageal region. Intestine commencing in XVII-XX, a dorsal typhlosole well developed. Body astomate, exonephric; caudally nephridial bodies enlarged, each with a pre-septal funnel; extensive tufting present in all or some of segments III-V. Enteronephry not developed. Holandric, sperm funnels free in X and XI, or metandric, the funnels in X absent. Seminal vesicles present in IX and XII, or in XI and XII. Prostatic glands tortuous tubes usually restricted to their segment of origin; posterior pair usually conspicuously smaller than the anterior set, or (*D. deminutionis*) totally lacking; prostatic ducts moderately long to long, muscularised. Penial seta follicles usually with copulatory musculature. Ovaries (conjoined oocytic strings) and medium-sized oviduetal funnels present in XIII; ovisacs. Spermathecae subequal, or the posterior pair slightly the larger; the single diverticulum is invariably sessile, and provided with numerous intramural sperm chambers.

DISTRIBUTION. Cape York Peninsula: apparently restricted to monsoonal semi-deciduous vine-forests in the Lockerbie, Iron Range and Weipa areas; islands of the Torres Strait (Fig. 1).

TYPE SPECIES. *Neodiplotrema tumida* (designated).

ETYMOLOGY. Differing from *Diplotrema* in a novel feature (meronephry).

REMARKS. The morphological similarities of *Neodiplotrema* to the Australian acanthodriline genus *Diplotrema* are so close, including even the possession of anterior genital setae in some species, that origin of the *Neodiplotrema* from the latter seems indisputable.

List of species of *NEODIPLOTREMA*

1) *N. deminutionis* sp. nov., 2) *N. exigua* sp. nov., 3) *N. lacisbrontoi* sp. nov., 4) *N. occidentalis* sp. nov., 5) *N. raveni* sp. nov., 6) *N. tumida* sp. nov., 7) *N. varionephrica* sp. nov.

KEY TO SPECIES OF THE GENUS *NEODIPLOTREMA*

1. Male apparatus acanthodrilin: 2 pairs of prostatic pores in XVII and XIX, male pores separate, on XVIII 2

   Male apparatus microscolecin: a single pair of prostatic pores associated with the male pores on XVII . . . . . *N. deminutionis*

2. Nephridia in the mid-body consisting of a prominent megameronephridium, and 3 small micromeronephridial bodies 3

   Nephridia in the mid-body uniform in size or mediannost nephridium not greatly enlarged . . 4

3. Genital setae present, intestine commencing in XVIII . . . . . *N. varionephrica*

   Genital setae absent, intestine commencing in XX . . . . . *N. exigua*

4. Male organs metandric . . . . . *N. occidentalis*

   Male organs holandric (though there may be some reduction in X) 5

5. Genital setae well-developed, in IX; prominent genital markings present in the region XVIII-XXI . . . . . *N. tumida*

   Genital setae absent or rudimentary. Genital markings absent from the region XVIII-XXI . 6

6. Moderately large worms (150-200mm); ventral setal couples of XVIII lacking, oesophagus with conspicuous outpouchings in XIV-XV . . . . . *N. lacisbrontoi*

   Very large worms (>350mm); ventral setal couples of XVIII present; oesophageal pouching absent . . . . . *N. raveni*

Neodiplotrema deminutionis sp. nov.
(Figs 2, 11B)

TYPE LOCALITY. 10°46'S, 142°34'E., on the eastern side of Lake Bronto, Cape York Peninsula, in open eucalypt forest in dark sandy soil. Coll. R. Raven, 4 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE AND 8 PARATYPES: ANIC GD.95.31.1

DESCRIPTION. Length 71+, 140mm. Width 2.9, 2.7mm. Segments 215+, 311 (Holotype, P2). Uniformly circular in cross-section throughout; pigmentless buff in alcohol. Prostomium prolobous, first dorsal pre-9/10. Setae in regular longitudinal rows, closely paired throughout; ventral setal couples of XVIII normal, those of XVII modified as enlarged penial setae; genital setae lacking. Nephropores inconspicuous. Clitellum not developed in any of the specimens available for study. Combined male and prostatic pores in distinct longitudinal slits on raised papillae, in

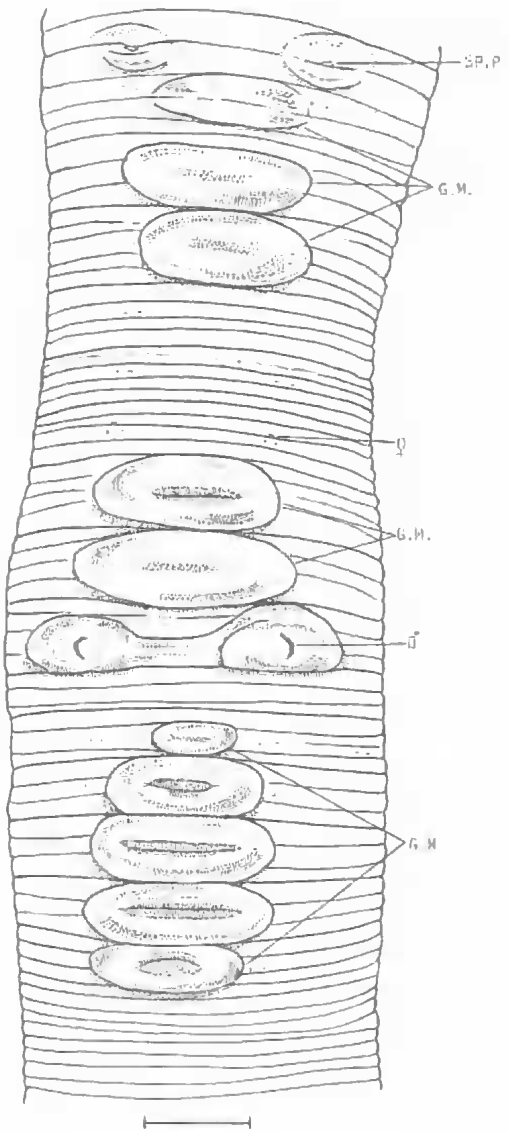

FIG. 2. *Neodiplotrema deminutionis* genital field.

XVII, coincident with the openings of the penial setae. Serial sectioning reveals that the vasa deferentia and prostatic ducts do not actually fuse, but open contiguously at the common pore. Female pores visible as tiny, transverse slits preseta lly, in *ab*, usually with swollen rims. Accessory markings a series of unpaired, median, intrasegmental pads: a small ellipsoidal pad in IX (H, P4-5); a larger one in X, extending across *aa* (H, P1-2, P4-5, P8); a similarly sized swelling in XI (H, P1, P6) (all the above markings have shallow, transversely concave centres); a large

pad is located in XV, transverse width = *aa* (H, P1, P3, P5-6), with a larger marking in XVI, across *bb* (all specimens excepting P7); another series of similar markings is present in the post-genital region: a diminutive tumescence in XIX (H, P1, P6), a much larger swelling in XX (across *aa*) (H, P1, P6), similarly in XXI (H, P1-6, P8), and a further small marking in XXII (H, P1, P2, P3, P4, P5, P6, P8). In some of the above specimens, the accessory markings are faintly developed.

Septa: 10/11, 11/12 slightly thickened, 6/7-9/10 moderately strongly muscularised, 5/6 slightly thickened, encapsulating the gizzard. Dorsal blood vessel single, continuous onto the pharynx. Supra-oesophageal vessel present VII-XIX, adherent to the roof of the oesophagus, and receiving vessels from oesophageal blood plexi, particularly in XII-XIV. Last hearts in XIII, those in X-XIII receiving thin connectives from the dorsal vessel, and more strongly developed ones from the supra-oesophageal vessels; commissurals XII and XIII much larger than the remainder, which decrease in size anteriorly, those anterior to X dorsoventral only. Gizzard large, shiny, but compressible in V, with a slight dorsoventral compression. Oesophagus rather narrow, constricted intersegmentally, with conspicuous rugae on its inner walls, and extending from VI to XVI. Intestinal origin, commencing with abrupt expansion, in XVII (H), XVI? (P1); somewhat paler and apparently less muscular anterior of XXIV. An extremely well-developed rugose dorsal typhlosole commences in XXII. Meronephric throughout; considerable tufting in IV, with many highly coiled loops, and composite ducts sent to the pharynx; the remainder of the nephridia comprised of very numerous astomate exonephric loops scattered on the body wall and septa, larger and more numerous in the oesophageal region. Caudally, the bodies again enlarged, each apparently with a distinct preseptal nephrostome; no enteronephry demonstrable.

Holandric; 2 pairs of small, iridescent funnels in X and XI, attached ventrally to septa 10/11 and 11/12; large, subequal, racemose seminal vesicles in XI and XII, anteriorly attached to septa 11/12 and 12/13, composed of large, conspicuous loculi. Vasa deferentia obvious as closely paired, slightly iridescent tubes tortuously adherent to the body wall on either side of the oesophagus; the paired ducts become fused in the parietes, in XVII. Prostatic glands a pair of flattened, loosely coiled tubular organs lying in segment XVII, with long, muscular (shiny) ducts opening to the exterior slightly ventral of the vasa deferentia. Penial seta follicles large, gently curving, copulatory musculature well developed, inserted near the mid-dorsal line; the setae with a gradual bend, the shaft divided into an ectal region devoid of ornamentation, with an intervening section bearing scattered solitary or clustered thorn-like spines with rather broad bases, and narrowing to a fine point (these stand out at an angle to the shaft); the entire ectal portion is approximately equal to the ornamented section, and these together constitute about half of the total length of the seta. Length mature seta 2.35mm; midshaft diameter 25.5µm (mean of 3). Ovaries, consisting of thin sheaves of small oocytes, together with medium-sized diaphanous funnels, are present XIII, ovisacs absent. Spermathecae a single pair, divided into a stalked, sacciform ampulla, and a broadly U-shaped diverticulum which is completely sessile, and which occupies the entire dorsal aspect of the short duct; the walls of the diverticulum are studded with numerous iridescent intramural sperm chambers; the ampullal 'stem' is swollen at its junction with the diverticulum. Length right spermatheca of IX 2.6mm (apex of ampulla to pore). Genital seta follicles absent.

ETYMOLOGY. Referring to the diminished (microscolecin) condition.

REMARKS. As this species is the only known microscolecin *Neodiplotrema*, identification should not prove difficult, particularly when the distinctive array of genital markings is also considered. The latter are atypical of the genus in being intrasegmental. *N. deminutionis* lives in sympatry with *N. lacisbrontoi* and *N. varionephrica*, but neither of these species appears to be convincing as an acanthodrilin precursor of the former.

Neodiplotrema exigua sp. nov.
(Figs 3, 11C)

TYPE LOCALITY. 10°48'S, 142°28'E, Lockerbie East, soil over rocky substrate, in dense semi-deciduous vine-forest. Coll. R. Raven, 1 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE. QMGH2889. PARATYPE. QMGH2890. OTHER MATERIAL. 10°48'S, 142°28'E, Lockerbie East, under logs near 'Mango Tree camp', Coll. R. Raven, 30 Jan 1975 (3 immature-semi-mature specimens, not designated as types, ANIC GD.95.9.3).

DESCRIPTION. Length 48, 64mm. Width (mid-clitellar) 1.7mm. Segments 149, 136 (Holotype, P1). Uniformly circular in cross-section,

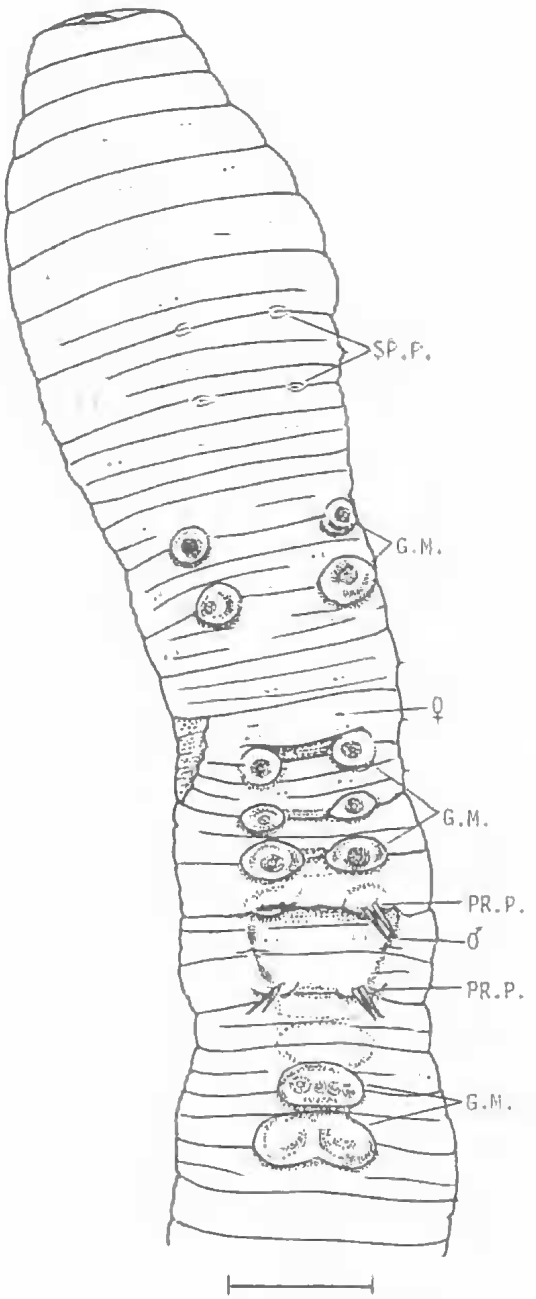

FIG. 3. *Neodiplotrema exigua* genital field.

pigmentless buff in alcohol. Prostomium prolobous; first dorsal pore 11/12 (imperforate). Setae 8 per segment, commencing in II; ventral setal couples of XVIII present; those in XVII and XIX modified as enlarged penial setae; genital setae lacking. nephropores not visible externally. Clitellum very faint, barely distinguishable. Male pores located presetally, in definite seminal grooves, on XVIII, lateral of *b*-lines. Prostatic porophores 2 pairs, in XVII and XIX, each on a distinct papilla, and intimately associated with (usually) protuberant penial setae. The slightly convex male field is delimited laterally by the seminal grooves (joining the prostatic pores of a side), with the prostatic porophores defining its corners. Female pores small slits presetal in XIV, in *ab*. Spermathecal pores 2 pairs of simple depressions, in 7/8 and 8/9, in *ab*. Accessory markings 2 pairs of rounded tumescences with oculate centres present intersegmentally, in 10/11 and 11/12. A further series of three more closely paired markings (of similar shape) present in 14/15 and 16/17, slightly lateral of *b*-lines; the markings in 14/15 are separated by a distinct depression, the remainder to a much lesser extent; a diffuse and indistinct pad extending from the posterior edge of the male field to the anterior portion of segment XXI is seen to be of width *bb*; 2 further unpaired median markings are located in 21/22 and 22/23, the former the smaller, with a multi-oculate central area, the marking in 22/23 longer, almost paired, with central depressions.

Septa: 5/6 delicate, 6/7-7/8 slightly thickened, 8/9-12/13 moderately muscularised, 13/14 slightly affected, remainder diaphanous. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X-XIII considerably larger than the remainder, with connectives from both the dorsal and supra-oesophageal vessels; the latter vessel moderately developed, its limits not determinable. Gizzard large, though compressible, in V; oesophagus narrow, VI-XIX, but with three pairs of obvious pouches in XVI-XVIII, that closely resemble stalked calciferous glands; these are complexly vascularised, and contain conspicuous lamellae; the three pouches on each side of the oesophagus are clearly interconnected, but communication of each of the pouches independently to the oesophagus could not be demonstrated. Intestinal origin XX, a robust, though flattened, dorsal typhlosole is present after XXV. Meronephric; the mid-body segments each containing a pair of large megameronephridia with preseptal nephrostomes, their terminal ducts discharging to a pair of ventral, longitudinal ureters that run the entire length of the body, opening at the anus; the megameronephridia decrease gradually in size posteriad, and disappear abruptly approximately 25 segments from the posterior end; in addition to the above, each intestinal segment contains 3

pairs of small, astomate, exonephric loops, distributed evenly on each side of the nerve-cord, the dorsalmost body just below the mid-dorsal line; these persist (perhaps with some slight trend towards a size increase) to the caudal extremity. A large pair of tufted nephridial bodies is present in V, with a much smaller set in VI.

Holandric; large, iridescent spermatic funnels and sperm masses seen in X and XI; 2 pairs of palmate seminal vesicles composed of large, slightly iridescent loculi present in IX and XII, the former somewhat smaller and compressed. Prostatic glands 2 pairs of simple tubular structures in XVII and XIX, the anterior pair the larger; the ducts are weakly muscular, and short. Penial seta follicles proportionately large for the species, each follicle with a distinct retractor ligament inserted on the dorsolateral aspect of the body wall. The setae fairly flat, gently curving, the ectal region with a distinct sinusoidal bend; the ectal 1/4-1/3 is ornamented with clusters of 1-4 irregular, jagged teeth. Length mature seta 2.4mm; midshaft diameter 53.4μm (mean of 3). Ovaries, comprising several strings of medium-sized oocytes, together with small, pleated oviducal funnels, present in XIII; minute rounded structures on the posterior face of septum 13/14 are questionably ovisacs. Spermathecae rather small, each organ consisting of an ovoid ampulla and sacciform, blunt diverticulum (with some iridescence); duct very short. Length right spermatheca of IX 0.6mm (base of ampulla to pore). Genital seta follicles absent.

ETYMOLOGY. Referring to the distinctive nephridial system.

REMARKS. This small species has undoubted affinities with *N. varionephrica*, both species possessing a remarkable nephridial system which incorporates a combination of micromeronephridia and megameronephridia, the latter with longitudinal ureters. This arrangement (as described in detail above) is reminiscent of that described by Bahl (1942) for the dichogastrin *Hoplochaetella khandalensis*, though in that species, the longitudinal ureters are located dorsally, and the megameronephridia continue to the extreme caudal segments. Bahl, in summarising nephridial modifications in earthworms, describes the condition whereby the common excretory canals open at the junction of the body wall and the gut (i.e., the anus) as '*the first steps, so to speak, in the enteronephric direction*' (Bahl (1947). An anatomical arrangement of the excretory system whereby longitudinal ureters terminate in the proctodaeal region is also seen in the Western Australian genus *Austrohoplochaetella* and the African species, *Millsonia anomala*. Jamieson (1974) detected significant intraspecific variation in the occurrence of meronephry in the Tasmanian species *Cryptodrilus polynephricus*, a further indication of the lability of this character-state.

The occurrence of this relatively advanced nephridial system in *Neodiplotrema* raises problems for the existing classification (Jamieson, 1971), in which, by definition, *N. varionephrica* and *N. exigua* would be placed in the Dichogastrini, within a different subfamily to that in which the bulk of *Neodiplotrema* species would be assigned. Apart from the nephridial modifications, which together with the absence of genital setae, serve to distinguish it from its congeners, *N. exigua* is otherwise unremarkable, there being little to justify the erection of a higher taxonomic category (i.e., a subgenus) to accommodate it and *N. varionephrica*.

Neodiplotrema lacisbrontoi sp. nov.
(Figs 4, 11D)

TYPE LOCALITY. 10°46'S, 142°34'E, dense rainforest at northern end of Lake Bronto, in openings in forest canopy, black sandy soil, dense leaf and twig litter, some ground cover, 1 m deep. Coll. R. Raven, 4 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE. QMG211957. PARATYPE. QMG211958 (4 specimens).

DESCRIPTION. Length 165+, 140mm (Holotype, P1). Width 4.9mm (H). Form circular in cross-section throughout, pigmentless buff in alcohol. Prostomium strongly furrowed. First dorsal pore at 9/10. Setae 8 per segment, closely paired, the ventral setal couples of XVIII absent; those of XVII and XIX modified as enlarged penial setae; the ventral setal couple on the left side of X very slightly enlarged, but cannot be regarded as functional genital setae. Nephropores not visible externally. Clitellum annular, fairly strongly developed over XIII-XVII (P1), setae visible. Male pores are situated just posterior to intersegment 17/18, lateral to *b*-lines; each surmounts a tiny papilla in a distinctly demarcated seminal groove, which connect the porophores on each side. Prostatic openings, 2 pairs, in XVII and XIX, not on distinct papillae, but rather at the anterior rim of small, circular concavities (more pronounced in the anterior pair), which form the four corners of a roughly square male field. In

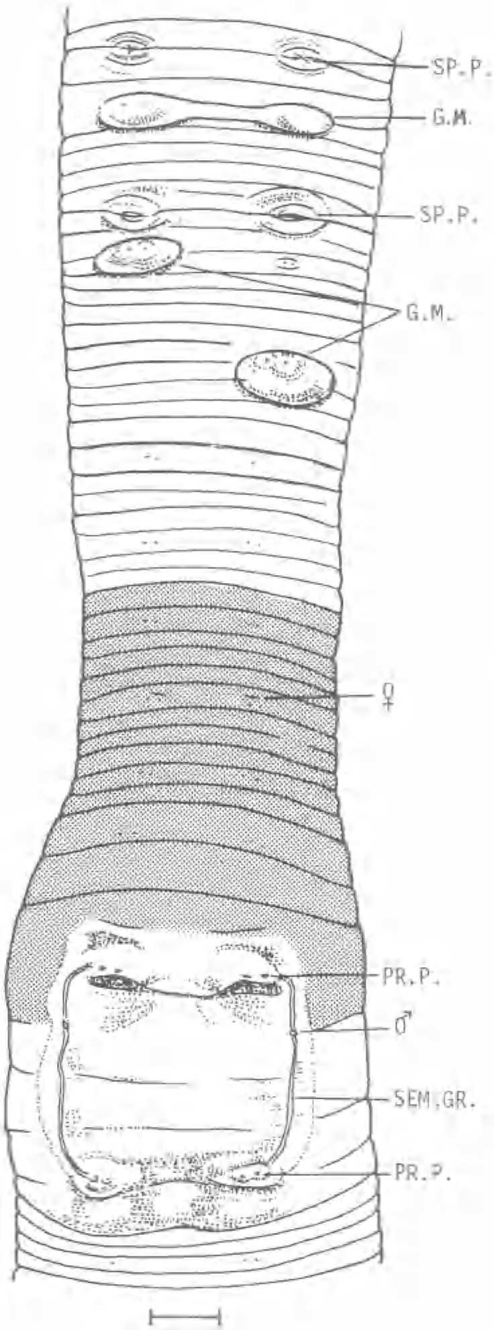

FIG. 4. *Neodiplotrema lacisbrontoi* genital field.

undissected specimens, this region appears slightly depressed with respect to the remainder of the body surface. Female pores are inconspicuous slits slightly pre-setal in *a* of XIV. Spermathecal pores 2 pairs in 7/8, 8/9, each with a conspicuously puckered rim. Accessory markings a very narrow tumid strip in XXI in *aa* with central depression; a similar marking in 20/21 without depression; a large tumescent patch in the upper portion of segment XVI, in *bb*; a papilliform swelling in X, centred on the left side ventral setal couple, but extending laterally in both directions, as well as anteriad and posteriad (P1 right side only, P2 present over both setal couples (reduced in size), P3 both sides, P4 right side only; a similar marking in IX, centred on *ab*, but confined within 2 adjacent intrasegmental furrows (H only); a pair of papilliform swellings in VIII, similarly disposed, but (H) conjoined by a median tumid band, P3 small papilla left side only, P4 left side only.

Septum 5/6 moderately thickened, septa 10/11, 11/12 strongly so, 6/7-9/10 very much thickened and muscularised. Dorsal blood vessel single, continuous onto the pharynx, where it divides repeatedly. Last hearts in XIII; those in XII and XIII the only large heart-like commissurals, the remainder being much reduced, and decreasing in size anteriorly; commissurals in X-XIII have thin connectives to both the dorsal and supra-oesophageal vessels; the latter is visible in segments X-XVI only, though ill-defined in segments X and XI. Gizzard very large, cylindrical and highly muscular, though somewhat compressible, in V. Oesophagus narrow, with conspicuous lateral pouching in XIV-XVI (in PI only present in XIV and XV); these outpouchings are internally lamellate, but their function is conjectural (calciferous, digestive, etc.); a further small dilatation of the oesophagus is present in XIII. Intestine commences with abrupt expansion in XVIII (XVII-P1), a definite double-ridged dorsal typhlosole present from XIX posteriad, being maximally developed from segment XXX. Nephridial system meronephric, in the forebody consisting of numerous, simple astomate, exonephric loops in each segment (more than 30 in the intestinal region); Caudally (i.e., the last 35-40 segments, the nephridial bodies of the last 15 or so segments being considerably enlarged. No enteronephry demonstrable; tufting present in IV, presumably enteronephric, but the composite ducts not traceable; the nephridial loops noticeably longer in V and the following oesophageal segments than in the intestinal region.

Holandric; 2 pairs small, highly convolute non-iridescent sperm funnels in X and XI, the former the larger; 2 pairs rounded, racemose seminal vesicles in XI and XII, the latter being obviously

the larger; (vice versa in P1). Vasa deferentia readily traceable on the body wall as a pair of closely associated tortuous tubes entering the parietes in XVII. Prostates, 2 pairs in XVII and XIX, each a narrow, highly coiled tube, restricted to its segment of origin, with a long, thick, looped muscular duct; the anterior prostates are invariably the larger pair. Medium-sized penisetal follicles, containing few reserve setae, present in XVII and XIX, associated with the prostatic ducts; extensive copulatory musculature (i.e., connective ligaturing of the follicles to the body wall, for the eversion and/or retraction of the penial setae during copulation) present. The setae robust, stout, somewhat flattened, the ectal end often twisted, the tip invariably recurved; the ectal 1/3 is ornamented with incomplete, staggered circlets of short, irregular toothlets. Length of mature seta 0.88mm; midshaft diameter 31.7μm (mean of 3). Ovaries fan-shaped, consisting of many strings of small oocytes, and these, together with medium-large oviducal funnels, are located in XIII. Spermathecae 2 pairs, in VIII and IX, each comprising a sacciform ampulla that is produced into a long digitiform projection (directed anteriad *in situ*), and a sessile, U-shaped diverticulum studded with large, iridescent, intramural sperm chambers; the diverticulum is embedded in the wall of the sac-like portion of the ampulla; length of right spermatheca of IX 2.9mm. Brain crescentic, with broad fusion of the supra-oesophageal ganglion; 2 quite distinct prostomial nerves arise close together at the point where the commissure widens to form the dorsal ganglion; these innervate different regions of the prostomium. Peristomial nerve single, but branching a short distance from its point of origin at the commissure (approximately midway between the sub- and supra-oesophageal ganglionic masses). Spermathecal genital setae absent; slightly enlarged setae are associated with the genital marking on left IX, but these are not specialised, and appear to be non-functional.

ETYMOLOGY. For the type-locality, Lake Bronto.

REMARKS. This species is distinguished from other forms in lacking genital setae, in having the male pores in an anterior position (near 17/18), and in exhibiting oesophageal pouching in the region XIV-XVI. Its closest affinities appear to lie with the much larger *N. raveni*, though this relationship is by no means close.

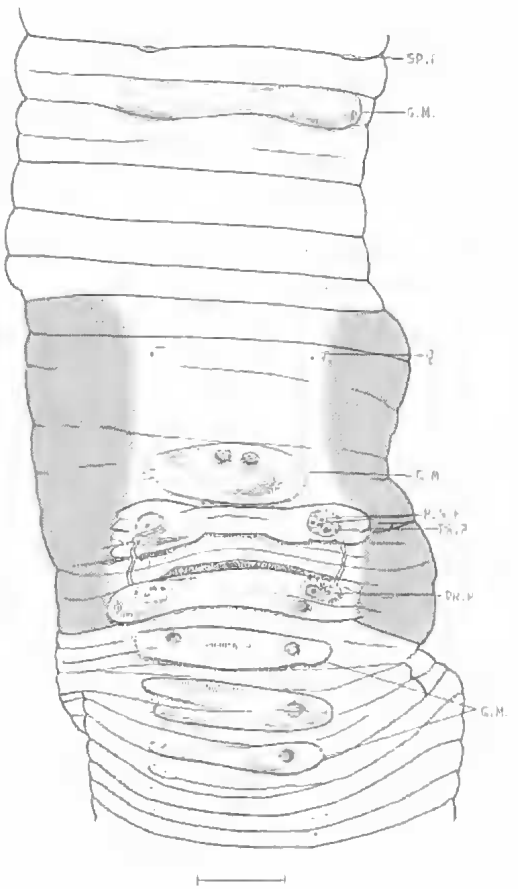

FIG. 5. *Neodiplotrema occidentalis* genital field.

Neodiplotrema occidentalis sp. nov.
(Figs 5, 11F)

TYPE LOCALITY. 12°35'S, 141°55'E, Weipa, north bank of the Mission River, Cape York Peninsula, in semi-deciduous vine-forest, litter layer 4-5cm deep, over black 'bauxite' soil. Coll. R. Raven, 7 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE. GD 75/44. PARATYPES. 2 aclitellate specimens. GD 75/45.

DESCRIPTION. Length 34+ (posterior amputee), 59mm. Width (midclitellar) 4.4, 4.2mm. Segments ?, 135 (Holotype, P1). Circular in cross-section throughout, pigmentless buff in alcohol, preservation poor (some maceration). Prostomium pro-epilobous, first dorsal pore 18/19 (H, P1). Setae 8 per segment, closely paired. Ventral setal couples of XVIII present; those of XVII and XIX enlarged as penial setae; genital

setae lacking. Nephropores not externally recognizable. Clitellum tumid, saddle-shaped, better developed dorsally, extending over segments XIII-XIX, the ventro-lateral limits indefinite. Male pores not definitely demonstrable (due to partial maceration), but presumed to lie within the shallow seminal grooves linking the prostatic pores of a side; the latter are atop tumid mounds that are connected across the ventrum by raised glandular strips. Each prostatic papilla bears 3 conspicuous pores; the two more closely associated openings marking the site of exit of the penial setae (as evidenced by the occasional protruding seta), whilst the remaining orifice is the prostatic opening proper. Female pores a pair of obvious slits close to seta *b* in XIV. Spermathecal pores inconspicuous in 7/8 and 8/9, aligned with *ab*. Accessory markings a series of single, median pads with paired pore-like centres: a marking in XVI, with the oculate dimpling closely paired, in the setal arc; a set of markings decreasing in lateral width posteriad, commences in XIX, immediately posterior to the prostatic porophores (confluent with the tumid strip linking the latter), and extends to XXII, the eye-like margins widely-spaced, not always present on the right side; a further slight swelling is present medianly in XXIII. The small protruberances in VIII, which overhand the spermathecal pores are apparently not associated with genital seta follicles.

Septa 5/6 diaphanous, 6/7 slightly thickened, 7/8-9/10 moderately thus, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, these commissurals being the only ones of any significant size, though those in XII are fairly robust; commissurals in XI-XIII demonstrably latero-oesophageal, with the supra-oesophageal vessel visible in segments X-XIII only. Gizzard large and firm, dolioform, in 5/6; oesophagus narrow, its length partially restricted by the posteriorly transgressive gizzard; intestine commences in XVI, no definite typhlosole noted. Meronephric throughout; a pair of very large tufts present in III, their composite ducts running anteriad to discharge into the buccal cavity; in the mid-body, each segment possesses approximately 10/12 scattered astomate, exonephric loops; caudally, the medianmost nephridium is enlarged as a megameronephridium (on each side), having a large, preseptal nephrostome; its ducts were not traceable owing to poor fixation; the remaining nephridia are smaller, astomate, and reduced in number (apparently only 3 on each side, regularly spaced).

Metandric; a single pair of faintly iridescent spermatic funnels that are nonetheless quite large, together with presumed testicular tissue (attached to posterior face of septum 10/11), seen in XI; the funnels are situated on septum 11/12, above the ventral body wall, with the vasa deferentia running down the septum and onto the peritoneum, where they are traceable as single, lazily winding ducts. A single large pair of seminal vesicles that are finely racemose are located in XII. Prostatic glands 2 pairs of very thin, flattened tubes, restricted to XVII and XIX, the anterior pair obviously the larger; the ducts are straight and poorly muscularised. Large, conjoined penisetal follicles containing numerous reserve setae, are associated with the ectal portion of the prostatic glands and their ducts; copulatory musculature is reduced to thin ligaments; the setae gently curving, tapering gradually to a rather blunt tip; the ectal extremity (approx. 1/5) ornamented with incomplete rows of very short, jagged toothlets, which become sparser proximally. Length of mature seta 1.63mm; midshaft diameter 34.2µm (mean of 2). Ovaries small, with minute funnels, in XIII, ovisacs not seen. Spermathecae 2 subequal pairs, in VIII and IX, each consisting of a bent, tubular ampulla, and sessile, reniform diverticulum, with ?radially arranged intramural sperm chambers containing innumerable brightly iridescent flecks. Length right spermatheca of IX 1.2mm (base of ampulla to pore).

ETYMOLOGY. For the type-locality at the western extremity of the known generic distribution.

REMARKS. The metandric condition of the male gonads, and the lack of genital setae, together with certain nephridial peculiarities, serve to characterise *N. occidentalis*. It is not known whether this species is linked through intermediate populations to the Lockerbie and Iron Range endemics, or is an interpluvial isolate. Semi-deciduous notophyll vine-thickets are very restricted in the Weipa region, usually located on well-drained sites where freshwater aquifers are close to the surface; if *N. occidentalis* is an obligate closed forest inhabitant, its range must necessarily be strictly limited.

Neodiplotrema raveni sp. nov.
(Figs 6, 11G)

TYPE LOCALITY. 10°48'S, 142°28'E, Lockerbie East, Cape York Peninsula, collected through formalin expulsion of very rocky, red lateritic soil; Coll. R. Raven, 2 Feb 1975.

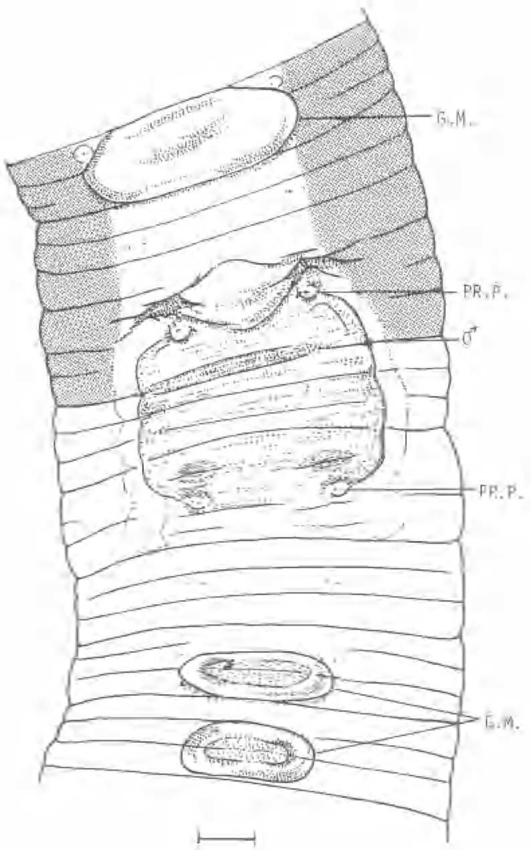

FIG. 6. *Neodiploirema raveni* genital field.

MATERIAL EXAMINED. HOLOTYPE. QMGH2951. PARATYPES. Paratypes 1 and 3 QMG211959; paratypes 2 and 4, ANIC GD 95.9.4.

DESCRIPTION. Length 465, 398mm. Width (midclitellar) 9.0mm, 6.8mm. Segments 457, 499 (H, P1). Circular in cross-section, pigmentless biscuit in alcohol. Prostomium pro-epilobous, peristomium much fissured. First dorsal pore 10/11 (H), 9/10 (P1, 4). Setae 8 per segment, in regular longitudinal rows throughout; ventral seta couples of XVIII present; those of XVII and XIX modified as enlarged penial setae; those of IX replaced by genital setae. Nephropores not seen. Clitellum saddle-shaped, weakly developed, over 1/2XII-XVII. Male pores inconspicuous, in the seminal grooves at 17/18, well lateral of *b*-lines; prostatic pores 2 pairs, in XVII and XIX, coincident with the penial seta orifices, on distinct mounds; the seminal grooves joining the pores of a side are very narrow, but deep, and are slightly convex laterally. The porophores lie in four distinctly sunken areas, which are transversely linked by two fairly broad channels, in XVII and XIX, the former of which is interrupted by a prominent cuneate tumescence in 16/17. The male genital area, bounded by the seminal grooves and the above-mentioned depressions, is concave with respect to the remainder of the body surface. Female pores inconspicuous openings well ventral of *a*, near 13/14. Spermathecal pores considerable, but located in deep intersegmental grooves, in 7/8 and 8/9, in *ab*. Accessory markings extensive torose tissue associated with the genital setae, in IX, forming a characteristic dumbbell-shaped tumid area (all specimens); a broad, pad present in X (H, P1-2), occasionally a similar marking in XI (P2); a series of elliptical pad-like markings (extending across *bb*) with transversely depressed centres seen in XXI (H - the smallest of the three markings), in XXII (H, P1/3, P2 - indistinct), and in XXIII (H, P1, P2 - indistinct); a broad pad, occupying much of the longitudinal dimension of XV, extends across *bb* (H, P1-2).

Septa: 5/6 moderately thickened, 6/7-10/11 much augmented with thick musculature (7/8-10/11 the strongest), 12/13 slightly thickened, remainder delicate. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, only the commissurals in XI-XIII large, heart-like, and receiving connectives from both the dorsal and supra-oesophageal vessels. The latter connectives are the more substantial; the supra-oesophageal vessel was noted in segments X-XIII only. Gizzard enormous, cylindrical, and virtually incompressible, in V; oesophagus completely suppressed by the posteriad encroachment of the gizzard in VI-X; thereafter highly vascular, but lacking pouching or calciferous glands. Intestine commences in XVIII, a strong dorsal typhlosole beginning abruptly at XIX. Meronephric throughout, nephridia commencing in II; very conspicuous, profusely divided tufts present in III and IV, their composite ducts running anteriorly, but not traced. The oesophageal region with large numbers of astomate, exonephric, sessile loops restricted to the parietes or the septal bases; these are fewer in number in the intestinal region, with a distinct concentration of bodies near the ventral nerve-cord; caudally, there is a multiplication and enlargement of the nephridial bodies, each apparently with its own preseptal nephrostome.

Holandric; wispy testis material and small-medium spermatic funnels (diaphanous, translucent-?non-functional) present in X and XI, testis-sacs absent; large, acinous, very finely divided semi-

nal vesicles present in XI and XII, the latter mass the larger. Prostatic glands 2 pairs of simple tubular organs restricted to, and extending laterally in, their segments of origin; the anterior pair is the larger. Each gland possesses a fairly long, coiled, muscular duct. The *a* and *b* follicles of the penial setae are indistinguishable, forming 2 pairs of stout, strongly curved bundles joined to the body wall in a number of places by copulatory ligaments. The setae broad, flattened, attenuating abruptly near the ectal end, the ectal extremity invariably recurved; the shaft with a faint scattering of very find clusters of short toothlets distally. Length of mature seta 3.43mm; midshaft diameter 123.9μm (mean of 2). Medium-sized, pleated oviducal funnels seen in XIII, small ?ovisacs attached to the posterior face of septum 12/13. Spermathecae 2 pairs, in VIII and IX, each organ consisting of a rounded diverticulum sessile on the body wall (duct virtually non-existent), and a regular, ovoid ampulla connected to the latter by a distinct, narrow peduncle; length right spermatheca of IX 3.8mm. Genital seta follicles a single pair, in IX, each containing several yellowish, slightly curved setae; these are ornamented over their ectal 1/3 not with scalloping, but with irregular transverse dentate grooves that are at the most 1/3 shaft circumference long. Length of mature seta 2.77mm; midshaft diameter 79.5μm (mean of 3).

ETYMOLOGY. For the collector, Robert Raven.

REMARKS. The lack of spermatozoal iridescence in the spermathecae or testis-segments in any of the specimens examined points to a parthenogenetic mode of reproduction for the species. *N. raveni* is a very large, deep-burrowing, distinctive species which is very readily identified, even in a comparatively juvenile state because of the peculiar bipartite spermathecae. It possibly also exists in the Torres Strait Islands in suitable habitats, but because of its burrowing habits, is would not be readily collected.

Neodiplotrema tumida sp. nov.
(Figs 7-8, 11E,H)

TYPE LOCALITY. ca. 10°48'S, 142°28'E, Lockerbie East, Cape York Peninsula, Coll. R. Raven. Holotype and paratypes 1, 3, 4: 2 Feb 1975; paratypes 5 and 6: 30 Jan 1975; paratypes 7-10, 11-17: 1 Feb 1975; paratypes 10, 18, 19: 3 Feb 1975.
10°35'S, 142°13'E, Green Hill, Thursday Island, in damp black clayey soil between rocks in vine-forest, paratypes 20-25, Coll. G. Berry, 7 Dec 1975.

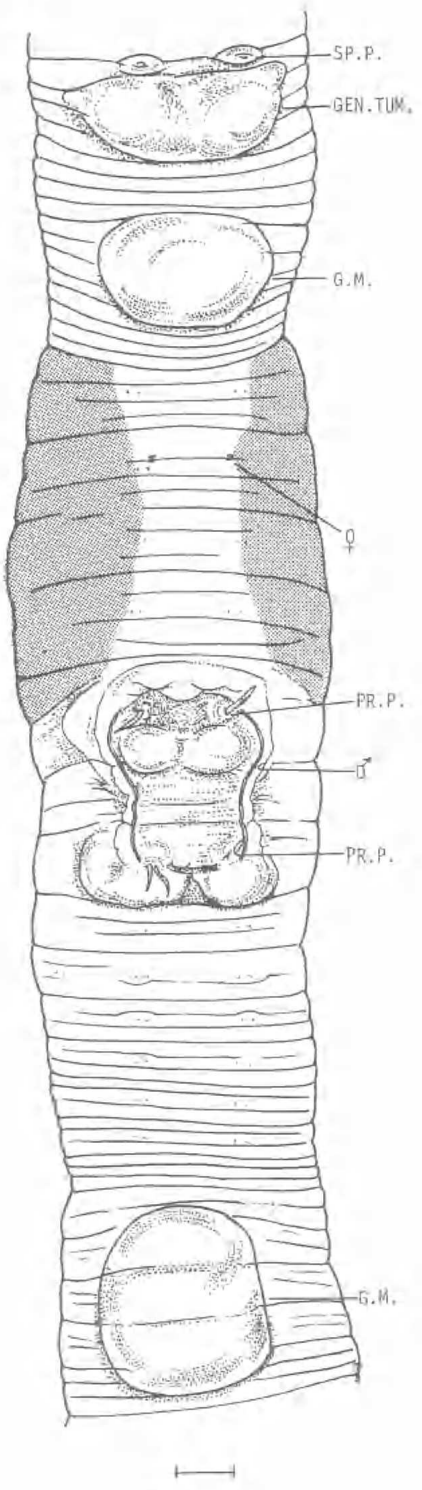

FIG. 7. *Neodiplotrema tumida* genital field.

MATERIAL EXAMINED. HOLOTYPE. ANIC GD.95.9.8. PARATYPES. P1, P3, P4, ANIC GD95.9.8; P5-6, ANIC GD.95.9.6; P11-13; P14, ANIC GD.95.9.7; P10, P18 & P19 (desiccated) ANIC GD.95.9.9.

DESCRIPTION. Length 149, 142.5mm. Width (midclitellar) 4.5, 3.4mm. Segments 282, 242 (Holotype, P1). Form circular in cross-section throughout, pigmentless buff in alcohol, clitellum in some specimens pink (P2, P4-6). Prostomium prolobous; first dorsal pore 8/9 (H, P1-2, P4) or 9/10 (P3). Setae 8 per segment, in regular rows throughout; ventral setal couples of XVIII absent; those in XVII and XIX modified as penial setae; those of IX as genital setae. Nephropores not conspicuous. Clitellum strongly-developed, saddle-shaped, over XIII-XVI (H. P1, P2-4); dorsal pores and intersegmental furrows distinct, setae obscured. Male pores slightly presetal, in narrow but deep seminal grooves that link the prostatic pores of a side; the latter are located in lateral depressions, separated by a central cuneiform tumescence; the posterior margins of the depressions in XVII and XIX are filled with 2 pairs of large, rounded swellings (anterior pair the larger), extending laterally to the seminal grooves, slightly beyond *b*-lines; segment XVIII slightly raised and traversed by deep intrasegmental furrows, and longitudinally seminal grooves, which turn ventrally to *b*-lines in XVIII. Female pores inconspicuous in a transverse furrow, just median of *a*-lines near intersegment 13/14, in XIV. Spermathecal pores very obvious on protuberant lips in *b*-lines, in 7/8 and 8/9. Accessory markings, a very large, swollen mound filling segment XI between the intersegmental furrows, and extending laterally beyond *b*-lines by a distance approximately equal to 2*bc* (all specimens); a similar tumescence extends over 3 segments (XXVIII-XXX), with some encroachment on segments XXVII and XXI; it is dissected by the intersegmental furrows of the segments it occupies (see thus in H, P7); XXVIII-XXIX only in P4, P8; XXIX-XXX only in P1, P2, P5-6, P9, P16, P17, P18); XXX-XXXI only in P3; a swollen mound associated with genital setae in IX, with similar proportions to the accessory markings in XI (H, P1-19). Accessory marking in XXXII only (P12, P12, P15, P19); XXVIII-XXIX only (P13); XXIX-XXX only (P11); XXXI-1/2XXXII only (P10); XXIX-1/2XXX1 only (P14).

Septa 11/12 moderately, 6/7-10/11 strongly mmuscularised, 5/6 only slightly thickened. Dorsal blood vessel single, continuous onto pharynx, where it divides repeatedly in III and IV. Supra-oesophageal vessel present, 1/2XI-XIV. Last hearts in XIII; those in XI-XIII the largest, receiving connectives from dorsal and supra-oesophageal vessels, the latter sending the larger connectives in XII and XXIII; the remaining commissurals decreasing in size anteriorly, and dorsoventral only. Gizzard large, highly muscular, and barrel-shaped, in V, with conspicuous

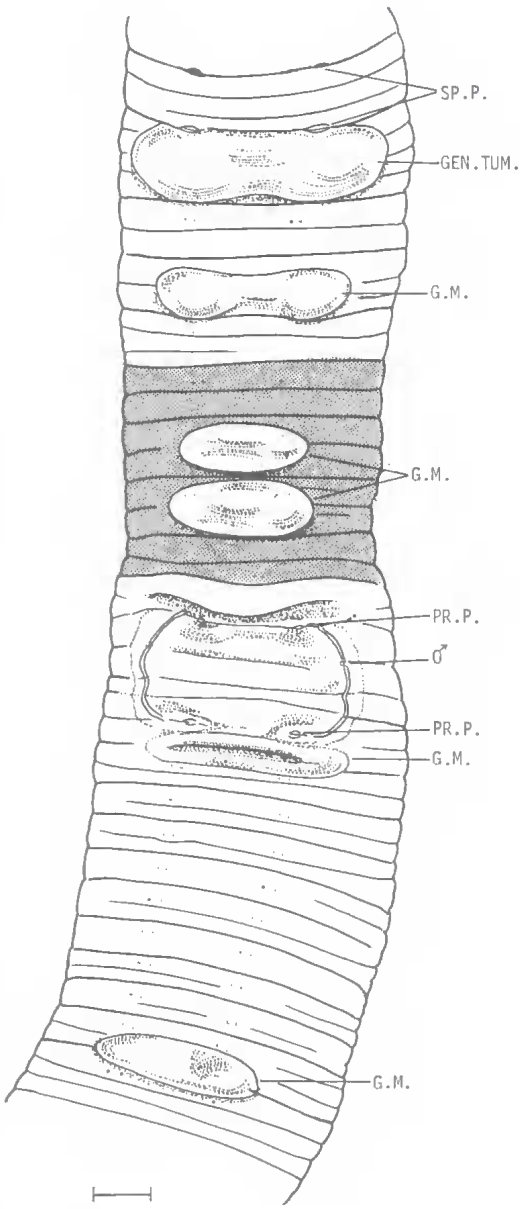

FIG. 8. *Neodiplotrema tumida* genital field.

midlength furrow. Oesophagus rather wide, thin-walled, in VI-XVI, vascularised to any extent only in XI-XVI; calciferous glands or pouching absent. Intestine commencing in XVII, with a low dorsal typhlosole commencing early, well-developed by XXV. Meronephric throughout; the pre-intestinal region with scattered astomate exonephric loops adherent to the body wall and septa, becoming more numerous in the intestinal region posteriad of XV (here the nephridial bodies are attached exclusively to the body wall); caudally with slight enlargement of the nephridial bodies each with a conspicuous pre-septal nephrostome (at least 8 counted on each side); robust pharyngeal tufting present in III and IV, the composite ducts not traced.

Holandric; small, iridescent, compactly plicate funnels and compacted sperm masses present in X and XI; loosely packed seminal vesicles with small, scattered loculi present in XI and XII. Prostatic glands small, flattened, tightly coiled tubular organs with origins in XVII and XIX, the latter pair much reduced (?becoming vestigial); a very long, coiled, muscular duct enters a lobulate glandular mass on each side in XVII, but these enter the parietes directly in XIX. Penisetal follicles conspicuous, and attached by ligaments to the body wall in XVII, the bundles reduced in size in XIX; the setae are fairly long, and bent into an arc; the distal portion is often twisted with respect to the main axis of the seta, the extreme ectal tip is invariably sharply recurved, uniform, the immediately posteriad portion of the shaft obviously thickened; the ectal of the shaft is ornamented with short, discontinuous rows of fine teeth, the rows arranged in a crude alternation. length of mature seta 2.29mm; midshaft diameter 77.0μm (mean of 2). Small ovaries, and medium-sized plicate funnels seen in XIII, ovisacs (?) attached to the posterior face of septum 12/13. Spermathecae 2 pairs in VIII and IX, the posterior pair readily perceived as the larger; each organ consists of a large, ovoid, bipartite ampulla, and a flattened, sessile, multi-loculate diverticulum occupying the dorsal aspect of the smaller ampullal portion; duct extremely short; length of right spermatheca of IX 2.7mm. A pair of small genital seta follicles present in IX (directed anteriorly, lying beneath the spermathecae); specialised glands lacking; the setae fairly straight, the ectal 1/5 distinctly ornamented with deep notching, the proximal rims of which are armed with irregular, sharp, triangular teeth. Length of mature seta 2.29mm; midshaft diameter 52.4μm (mean of 3).

ETYMOLOGY. For the large ventral genital tumescences.

REMARKS. The Thursday Island specimens differ in a number of respects from the Lockerbie forms, almost to the extent that subspecific rank might be warranted. There are, however, unusual morphological features common to both that signify close relationship. The major divergences from the type description exhibited by the Thursday Island forms are as follows: Length 140-175mm; width (midclitellar) 4.4-4.7mm; segments 313-324; first dorsal pore 9/10-11/12. Accessory markings a large, tumid pad extending across *cc*, and filling segment IX longitudinally (P20-21); a pair of mounds or composite bipartite tumescences post-setally in XI, extending laterally to mid-*bc* (P20-21) and XV (P20, P22); a large, median tumid pad occupying most of segment XXVIII and the extreme anterior portion of XXIX (P20-21). Supra-oesophageal vessel seen in X-XVI; intestine commences in XIX; typhlosole commences immediately, but enlarges abruptly in XXXI as a complex, 4-folded structure; posterior prostatic glands not much reduced (as for mainland specimens); spermathecal ampulla bent, slightly bulbous ectally, the diverticulum a sessile tubercle on the bulbous portion of the ampulla. Length right spermatheca of IX (base of ampulla to pore 2.6mm).

The presence of genital setae in IX, the location of the male pores in 17/18, the occurrence of a large genital pad in the vicinity of XXVIII-XXXI, and the terminally bulbous, hooked penial setae are all characteristic of *N. tumida*, and may be used in combination to confirm identity. Immature material from Horn Island may also be referable to this species, a further indication that it is comparatively widespread. Little divergence has apparently occurred since the presumed separation of the mainland from Thursday Island populations after the drowning of Torres Strait, approximately 6,500-8,000 years bp. The duration of insular isolation is approximately equivalent to that experienced by mainland and Melville Island populations of *Diplotrema ridei* in the Northern Territory, though overall morphological divergence is slightly more pronounced in the latter case.

Neodiplotrema varionephrica sp. nov.
(Fig. 9)

TYPE LOCALITY. 10°46'S, 142°34'E, Eastern side of Lake Bronto, approximately 10 km from the tip of Cape York Peninsula, in dark sandy soil in open *Euca-*

lyptus dominated forest, with dense ground cover. Coll. R. Raven, 2 Feb 1975.

MATERIAL EXAMINED. HOLOTYPE. QMGH2952. PARATYPES. QMGH2953. OTHER MATERIAL. Lake Bronto, on eastern side of lake, open eucalypt forest, much ground cover, dark sandy soil. One specimen registered as QMG211960; 11 further specimens registered as QMG211961.

DESCRIPTION. Length 43, 42+ mm (posterior amputee). Width (midclitellar) 3.1, 3.0mm. Segments 155, 110+ (Holotype, P1). Form circular in cross-section throughout, pigmentless grey-buff in alcohol, clitellum a slight pinkish-brown. First dorsal pore 11/12 (H, P1), prostomium proepilobous. Setae 8 per segment, commencing in II, in regular longitudinal rows throughout; ventral couples of XVIII absent or much reduced; those of XVII and XIX modified as enlarged penial setae; those of X replaced by genital setae. Nephropores not visible externally. Clitellum annular, more pronounced dorsally, over XIII-XVIII; dorsal pores obscured, intersegmental furrows only visible ventrally. Male pores small slits located in the relatively broad seminal grooves linking the porophores of a side; the male openings are well lateral of *b*-lines, located approximately midway between the setal arc and 17/18; prostatic pores 2 pairs, in XVII and XIX, each on a slight protruberance overhanging a deep transverse fissure. Female pores small slits barely presetal, median of *a*-lines by the distance *ab* 1 in XIV. Spermathecal pores in 7/8 and 8/9, in *a*-lines, the slit-like pores inclined at a slight angle to the plane of the intersegmental furrows. Accessory markings a conspicuous tumescence associated with the genital setae present in X (H, P1-left side only, P2 left side only). A series of 6 pairs of ellipsoidal intersegmental markings with oculate centres commencing in 10/11 (H, P1-right side only, P2, P3-left side only, P4-11), in 11/12 (H, P1-11), in 12/13 (H, P5-right, P6-right, P9, P11), in 13/14 (H, P1-7, P9-11), in 14/15 (H, P1-5, P6-right, P7-11), in 15/16 (H, P1-10) and in 16/17 (H, P1-11). A broader tumid pad extends laterally to *b*-lines to fill segment XIV between the intersegmental markings at 13/14 and 14/15 (H, P1-2, P3-weak, P4-11); a similar transverse marking may be present in XX (to *b*-lines) seen in P3-4, P7, P9 (weak), P10-11; a transversely elliptical pad in 21/22, extending laterally to slightly beyond *b*-lines is often present (H, P5-6, P10-11), with a similar marking less commonly occurring in 22/23 (P6-7 only); exceptionally, there is an additional marking similar to those in the clitellar region in 20/21 (P10, right side only).

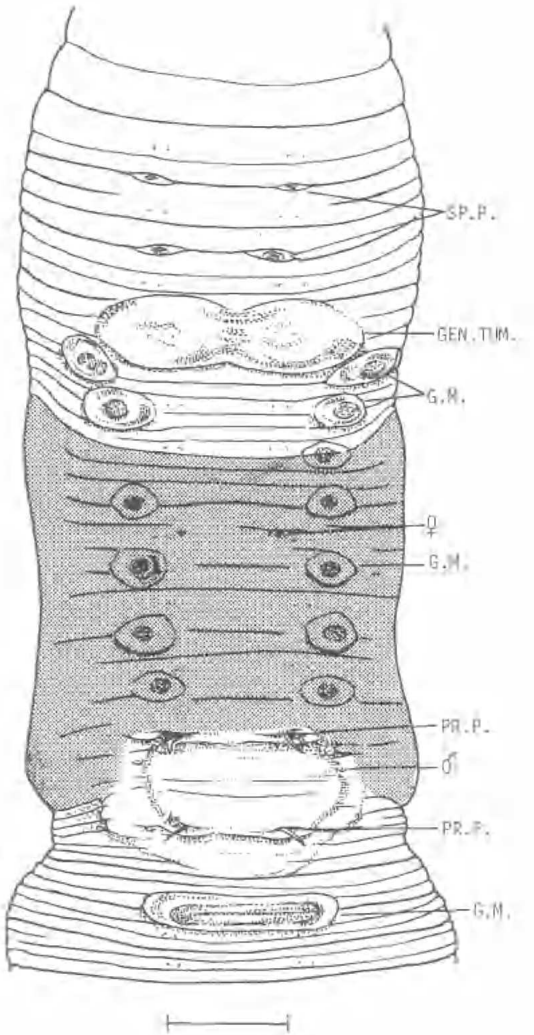

FIG. 9. *Neodiplotrema varionephrica* genital field.

Genital seta location variations: located in VII (P3, left side only, P8, left side only), in VIII (P4-5), and in IX (P3, left side only). No accessory markings corresponding to genital seta locations were detected in P5-7, P9-11.

No septa strongly muscularised, but 6/7-10/11 slightly thicker than the remainder. Dorsal blood vessel single; last hearts in XIII, those in X-XIII with thin connectives received from the dorsal and supra-oesophageal vessels; the latter vessel is detectable in IX-XIII. Gizzard large, well-developed, though compressible, in V, with a softer proventricular portion; oesophagus fairly short, somewhat compressed due to the posteriad transgression of the gizzard (septa to 12/13 directed

posteriad as a result of the latter); oesophagus well vascularised, with conspicuous rugae on its inner walls; 3 pairs of large, lateral outpouchings present in XVI-XVIII, containing definite lamellae, but all interconnected, with a single narrow opening leading to the oesophagus proper in XVII. Intestinal origin at posterior end of XVIII, a strongly developed dorsal typhlosole commencing in XXIV. Meronephric; large tufts developed in V, their composite ducts passing anteriorly to the buccal cavity; smaller clusters of loops seen in IV and ?III; the oesophageal region with approximately 6 small astomate, exonephric loops on each side; in segment XX, a conspicuous megameronephridium developed on each side, with a large preseptal nephrostome, and long excretory duct discharging into a thin-walled ureter running the length of the body on either side of the ventral nerve-cord, in *ab*; in addition, 3 small micromeronephridial loops are retained on each side of a segment: one in *bc*, with minute ducts entering the parietes in *b*-lines, an intermediate lateral loop above *d*, and a dorsal body close to the middorsal line (the latter are all astomate and exonephric); this arrangement persists to the extreme caudal segments, the ureters apparently discharging at the anus; the megameronephridia are lost some 30 segments from the posterior end.

Holandric; compacted sperm masses and medium-sized iridescent funnels seen in X and XI; 2 pairs of seminal vesicles, consisting of large, loosely associated loculi, present in IX and XII, the posterior set much larger. Prostatic glands 2 pairs of relatively small, simple tubular structures with short, muscular ducts, restricted to XVII and XIX; penisetal follicles rather small, but densely packed with reserve setae; a single band-like ligature passes across the prostates to link the follicles to the body wall near the mid-dorsal line. The setae gently curving, the tip invariably with a very distinctive trilobate appearance, the ectal 1/4 of the shaft bearing an irregular scattering of thorn-like (slightly recurved) spines. Length of mature seta 1.04mm; midshaft diameter 44.3μm (mean of 3). Ovaries consist of flabelliform clusters of oocytes; these and medium-large oviducal funnels are present in XIII; no ovisacs seen. Spermathecae consisting of an ovoid ampulla and a short, blunt diverticulum containing a number of iridescent intramural pockets. Length right spermatheca of IX 1.2mm. Genital seta follicles usually located in IX, no glandular structures associated; the follicles have some copulatory musculature; the setae are fairly straight, ornamented over the ectal 1/2-1/3 with regular notching.

ETYMOLOGY. Referring to the highly diverse nephridial system.

REMARKS. This species is closely allied to *N. exigua*, the major synapomorphic character being the peculiar nephridial arrangement (mixed mega- and micromeronephridia in the mid-body, with ureters). *N. varionephrica* may be distinguished on the basis of its very distinctive penial setae, which, unlike any known Australian acanthodrile, possess trifid tips. Other somatic characters, such as the position of the first intestinal segment, and the presence or absence of genital setae may also be used in conjunction with penial seta morphology to identify the species.

Genus **Torresiella** nov.

DIAGNOSIS. Setae eight per segment, prostates a single pair in XIX; male pores a single pair combined with the latter, on XIX. Spermathecal pores a single pair, ventrolateral, in 7/8. Wholly meronephric, with astomate exonephric nephridia throughout; tufting present in the pharyngeal region. Gizzard well-developed, in V. Calciferous glands absent. Holandric, testis-sacs absent. Penial setae and genital setae present.

DESCRIPTION. As for the type-species.

TYPE-SPECIES. *T. singularis* (monotypic).

ETYMOLOGY. Referring to the type locality in Torres Strait.

Torresiella singularis sp. nov. Dyne
(Figs 10, 11A)

TYPE LOCALITY. 10°37'S, 42°17'E, Horn Island, Torres Strait, 0.4km east of the airstrip, in moist clay near eucalypts, beside a narrow creek. Coll. R. Raven, 27 Jan 1975.

MATERIAL EXAMINED. HOLOTYPE. QMGH2936. PARATYPE. QMGH2937.

DESCRIPTION. Length 74, 92mm. Width (midclitellar) 3.4, 3.3mm. Segments 164, 202 (approximate due to maceration). Uniformly circular in cross-section, pigmentless grey in alcohol. Prostomium prolobous, peristomium with a dorsal cleft. First dorsal pore 8/9. Setae 8 per segment, commencing in II; caudal setae conspicuously enlarged with respect to the other somatic setae; ventral setal couples of XIX modified as enlarged penial setae; those of XVII and

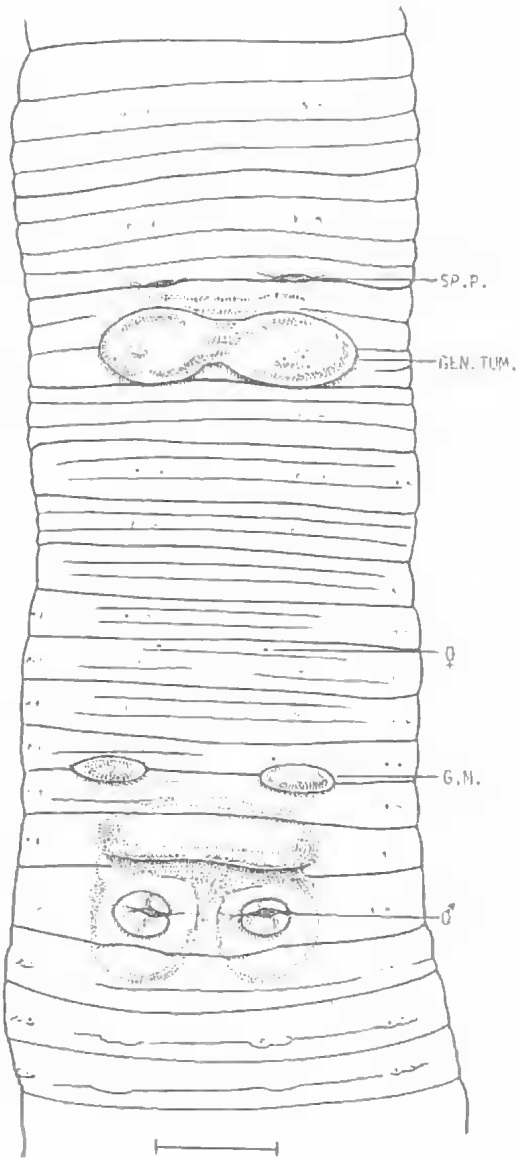

FIG. 10. *Torresiella singularis* genital field.

XVIII lacking. Nephropores not externally recognizable. Clitellum not developed. Combined male and prostatic pores in *ab* on XIX, coincident with the penial seta orifices. The combined pores are located on low mounds, the anterior and posterior approaches of which have a darker, glandular appearance; the male field generally depresses, with a conspicuous furrow at 18/19, overhung anteriorly by a lightly tumid region aeross *bb*. Accessory markings slight tumid swelling associated with the development of genital setae usually present in VIII, below the spermatheeal pores. Female pores minute points presetally, in an intrasegmental furrow, median of *a*-lines, in XIV. Spermatheeal pores a single pair, in *ab*, in 7/8, conspieuous as expanded, rimless orifices.

Septa: 5/6 delieate, 6/7, 7/8, 8/9 with a slight-moderate thickening, 9/10-10/11 moderately muscularised, 11/12 slightly so. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, those in X-XIII larger than the more anterior commissurals, and with connectives to both the dorsal and supra-oesophageal vessels (the remainder dorsoventral only); supra-oesophageal vessel weakly developed, widest in XIV, not traceable anteriad of VIII. Gizzard moderately large, muscular, dolioform, compressible, in V; oesophagus in VI-XVI, fairly wide, well supplied with blood vessels, dilating slightly intrasegmentally; expanded into broad outpouchings in XIII-XIV, not demarcated from the lumen, or calciferous gland-like. Intestine commences with gradual expansion in XVII, a strongly developed dorsal typhlosole present after XXV. Meronephric throughout; numerous, scattered, astomate, exonephric loops present on the parietes throughout, more numerous in the intestinal region. Caudally, with some slight inerease in size, but with no evidence of nephrostomes or enteronephric development. A small tuft occurs in IV.

Holandric; 2 pairs of small, slightly iridescent spermatic funnels in X and XI, with 2 pairs of small, loosely compacted seminal vesieles in IX and XII; vasa deferentia non-iridescent, clearly visible only in the 3 segments immediately preceding the prostatic segment; still paired on each side in XVIII, fusing in XIX, and entering the parietes simultaneously with the prostatic duet, ?fusing with the latter at this point. Prostatic glands small organs, situated far laterally in XIX, extending into XX, with a few loose coils in the horizontal plane; the muscular duct of uniform diameter, long and straight, perhaps as long or longer than the uncoiled glandular portion, entering the parietes in XIX, through a glandular mass. Penial seta follicles conspicuous, *a* and *b* components distinguishable, each with only 2-3 yellowish setae; the follieles are attached to the body wall by a large band of retraetor musculature passing across the prostatic glands, and attached by several strands in 20/21. The setae with a very straight shaft, cetally with a charaeteristic unci-

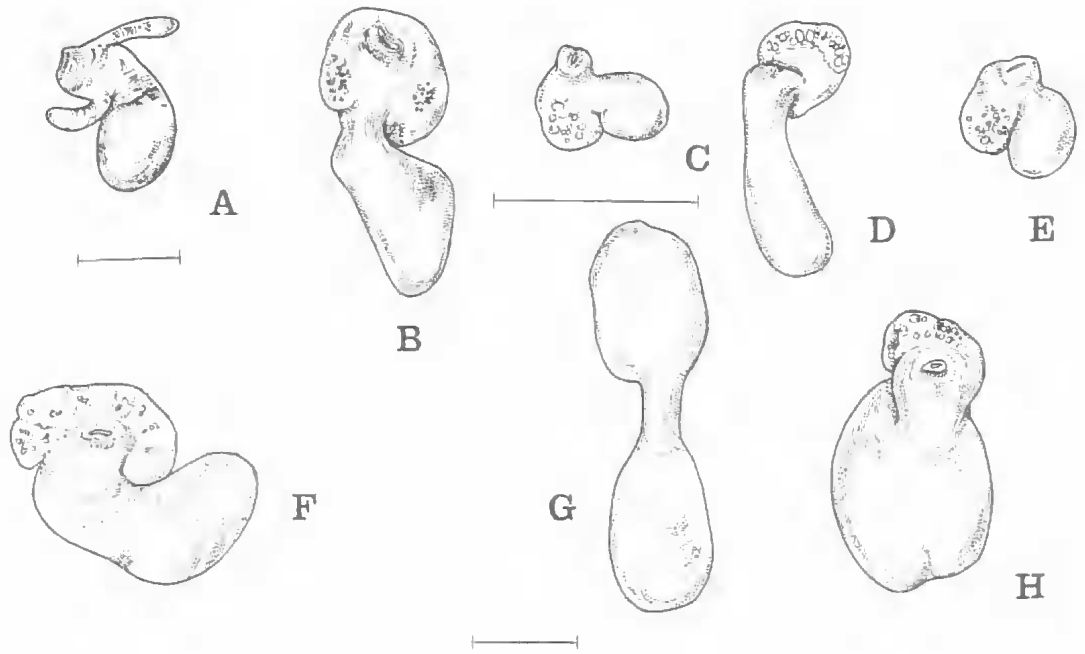

FIG. 11. A, Spermatheca of *Torresiella singularis*. B, Spermatheca of *Neodiplotrema deminutionis*. C, Spermatheca of *Neodiplotrema exigua*. D, Spermatheca of *Neodiplotrema lacisbrontoi*. E, Spermatheca of *Neodiplotrema varionephrica*. F, Spermatheca of *Neodiplotrema occidentalis*. G, Spermatheca of *Neodiplotrema raveni*. H, Spermatheca of *Neodiplotrema tumida*.

nate appearance; ornamentation restricted to a small region behind the point where the shaft begins to curve sharply, consisting of densely packed, short clusters of jagged teeth. Ovaries small, the ovarian funnels diaphanous, medium-sized, located in XIII; a pair of botryoidal ovisacs present, attached to the posterior face of septum 13/14. Spermathecae a single pair, in VIII, each consisting of a pyriform ampulla, divided into 2 sections by a transverse constriction, and two discrete, clavate diverticula joining the ectal ampullal region; duct indistinguishable from the latter. Length of right spermatheca 2.1mm (the diverticula may be terminally bifid). Genital seta follicles present in VIII, with attached musculature, but no glandular structures. The setae angular in cross-section, fairly straight, the ectal 1/2-1/3 of the shaft conspicuously ornamented with dentate notching.

ETYMOLOGY. Referring to the monotypic nature and the rare balantine condition of the genus.

REMARKS. *T. singularis* is the only known balantine Australian acanthodrile.

DISCUSSION

Neodiplotrema contains species with nephridial systems that by previous definition — having a pair of stomate meronephridia median to astomate micromeronephridia caudally — would be considered to place it in the Dichogastrini, in the subfamily Megascolecinae. The genus is here excluded from the Dichogastrini because of the obvious independent origin of its excretory apomorphy, as evidenced by the undoubted close relationship of its species to those of the holonephric genus *Diplotrema*, in the subfamily Acanthodrilinae (Tribe Acanthodrilini). The classificatory problem raised by the convergent development of complex meronephric systems in the Acanthodrilini (sensu Jamieson, 1971) demonstrated in this paper will need to be addressed more broadly, with particular attention given to the validity of the Dichogastrini as a grouping. Jamieson (1978) has already shown, in a cladistic analysis, that *Dichogaster* (Dichogastrini) grouped with a meronephric *Diplotrema* sp. (now *Neodiplotrema*; Acanthodrilinae) and stated that this grouping tended to confirm his suspicion that

'those Dichogastrini with acanthodrilin male pores (India and Africa) are descended from Acanthodrillinae and are distinct from dichogastrins with megascolecin male pores (Oriental and Australia)'.

Torresiella is also meronephric and appears to be a related to the *Diplotrema-Neodiplotrema* assemblage. Balantine reduction (male pores migrating posteriorly to unite with a single pair of prostate pores, in XIX), which distinguishes *Torresiella* from all other Australian acanthodriles, is a much less common phenomenon than is the microscolecine transformation (male pores migrating forwards to unite with a single pair of prostate pores, in XVII). The term derives from a meronephric West African species described by Michaelsen in 1898 for which he erected a new genus, *Balanta*. This was on the basis of the combined male and prostatic pores being located on XIX, an arrangement that had not previously been recorded. Only two years later, in 'Das Tierreich', Michaelsen (1900) suppressed *Balanta* in *Dichogaster*, as its only species, *B. ehrhardti*, had close apparent affinities to other members of that genus, despite the acanthodriline apparatus of the latter.

Other balantine genera include *Balanteodrilus* (monotypic) recorded from Yucatan Caves by Pickford (1938), and *Sylvodrilus*, a New Zealand taxon. Partial balantine reduction is known from *Udeina* (*U. montanus*) and *Pickfordia* (*P. hemibalantina* Omodeo, 1958); in these species, the posterior prostates are retained, but the male pore has not migrated, remaining in XVIII. In *Sylvodrilus*, the male pores have shifted to the posterior part of XVIII, and in *Balanteodrilus*, they are located in 18/19. The most advanced degree of transformation is thus to be found in *Torresiella*, in which the male and prostatic ducts are intimately associated (?fused) behind the combined pore. This condition is approached in *Dichogaster ehrhardti*, where, according to Michaelsen (1898): *'... der Samenleiter ... in die vordere Flache einer winzigen, atrium-artigen Hypodermis-Einsenkung ausmundend, in deren Grunde der Prostataporus liegt'*.

Why the balantine condition should be so rare is not known. In the acanthodrile genera examined by the author, there is a distinct tendency for the anterior prostatic glands to be conspicuously larger than the posterior organs. Correspondingly, the anterior spermathecae are often smaller than those posterior. Again, there is no satisfactory explanation for these observations, but they do indicate a certain predisposition to the microscolecin reduction. Intermediate stages in reduction suggest that in either reduction, elimination of one of the prostatic sets is a gradual process. The migration of the terminal end of the vas deferens must be largely influenced by the differential effects of the two prostatic pairs. This is presumed to be an embryonic phenomenon, the relative size of the prostatic primordia having a deterministic effect on the length of the vas deferens and the positioning of the male pore (the 'balanced' effect of subequal prostatic sets resulting in an equatorial or slightly presetal position of the male pore, as is commonly the case). A gradualist interpretation, where the male pore migrates progressively over many generations owing to some external selective force, though difficult to accept, appears to be appropriate in this instance. In cases where the male pore fails to migrate despite elimination of either prostatic pair, stabilising selection or some other influence may be involved.

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